NeoBiota 36: 39–55 (2017)
doi: 10.3897/neobiota.36.14953
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Comparing functional traits and abundance of invasive versus native woodwasps

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Academic editor: *A. Roques* | Received 9 July 2017 | Accepted 25 September 2017 | Published 3 November 2017

Citation: Hajek AE, Henry JC, Standley CR, Foelker CJ (2017) Comparing functional traits and abundance of invasive versus native woodwasps. NeoBiota 36: 39–55. https://doi.org/10.3897/neobiota.36.14953

Abstract

Functional traits are useful for comparing the resource use of invasive and native species, with goals of identifying resource overlap to predict competitive interactions. The invasion of northeastern North America by the woodwasp *Sirex noctilio* has resulted in competition with the native congeneric *Sirex nigricornis* for suppressed and weakened pines. We compared sizes of adults, venom glands, fecundity, tree species use, voltinism and abundance of the invasive woodwasp *S. noctilio* with the native *S. nigricornis* in northeastern North American pines. Rearing adults from attacked pines showed that these species used the same tree species but *S. noctilio* were far more abundant, especially with increasing time since establishment. Adults of the invasive *S. noctilio* were larger than *S. nigricornis*, female *S. noctilio* had larger glands carrying phytotoxic venom in relation to body size, average-sized *S. noctilio* females carried more eggs, and *S. noctilio* developed faster than *S. nigricornis*. *Sirex noctilio* was the dominant woodwasp infesting suppressed pines in our study areas. We hypothesize that the future abundance of *S. nigricornis* could depend in part on the availability of wood for oviposition by this native that is not available or acceptable to the earlier-emerging *S. noctilio*.

Keywords

invasive species, functional traits, Siricidae, wood borers

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Introduction

A major cause of global change is the pervasive introduction of alien species (Wardle et al. 2011; Simberloff et al. 2013) and the increase in global biotic homogenization is not predicted to diminish any time soon (Seebens et al. 2017). Once established in new locations, alien species with strong impacts can change ecosystems in many ways, including altering the biology and ecology of native competitors. The results from interactions between invasive and native competitors can range between coexistence, survival by differential use of resources that arise occasionally or periodically, and competitive displacement of the native species that can remain at low densities or become extinct (see Boivin et al. 2008).

The nature and extent of ecological impacts of alien species depend on the functional ecology of these species in the context of the structure, diversity, and evolutionary experience of the recipient community (Ricciardi et al. 2013). Evaluation of functional traits of invasives and co-existing natives is one means for understanding the effects of invasions, and especially the extent that an invasive is impacting native communities (Mouillot et al. 2013). Although impacts must be evaluated in the context of communities, functional traits such as rapid exploitation of resources and elevated fecundity have been associated with high-impact invasives (Ricciardi et al. 2013). Invasive species that have the greatest impact have also been suggested as being those introducing novel traits and becoming dominant members of communities (Rodriguez-Cabal et al. 2015; Callaway and Ridenour 2004).

Arthropods constitute the most diverse group of organisms (Pimm et al. 1995) and our understanding of the biologies and ecologies of the majority of native species in native ecosystems is frequently limited for many arthropod species prior to invasions. Yet, invasive arthropods have had and are presently having enormous impacts in forests (Liebhold et al. 1995; Gandhi and Herms 2010). Woodwasps are generally not considered forest pests and relatively little is known about their functional traits, although the aggressive invasive *Sirex noctilio* is a major exception. *Sirex noctilio* is not a pest where it is native in Eurasia and North Africa, but has caused economic damage in plantations of exotic pines (*Pinus* spp.) after introductions in the southern hemisphere (Slippers et al. 2015). Established populations of *S. noctilio* were first reported in northeastern North America in 2004 (Hoebeke et al. 2005) and this invasive now occurs in eight eastern US states (CERIS 2017) and two eastern Canadian provinces (de Groot et al. 2006, CFIA 2009) and it is expected to continue to spread. In the southern and northern hemispheres, *S. noctilio* typically oviposits in suppressed pines (Neumann and Minko 1981, Dodds et al. 2010; Ayres et al. 2014). However, populations can increase and, especially in overstocked stands and during droughts, *S. noctilio* can kill pines that are considered healthy (Madden 1988). *Sirex noctilio* kills pines by injecting an obligate symbiotic white rot fungus, *Amylostereum areolatum* (Ryan and Hurley 2012), and a phytotoxic venom (Bordeaux et al. 2014) in association with laying eggs into trees. Wood-boring *S. noctilio* larvae can only develop if the white rot fungus is present, as it serves as an external rumen for larvae (Thompson et al. 2014).

The establishment of *S. noctilio* in eastern North America is the first time that this invasive has invaded an area hosting native *Pinus* and *Sirex* communities, including the congeneric native pine-specialist *S. nigricornis* which has never been considered a pest in North America. *Sirex nigricornis* is associated with one of two fungal symbionts: either the same fungal symbiont as *S. noctilio* (*A. areolatum*) or *Amylostereum chailletii* (Hajek et al. 2013; Olatinwo et al. 2013). *Sirex nigricornis* can co-occur in pines with *S. noctilio* (Ryan et al. 2012a; Hajek et al. 2013). Most adults of *S. nigricornis* emerge to mate and oviposit approximately 1-2 months after *S. noctilio* (Ryan et al. 2012a; Foelker et al. 2016; Suppl. material 1: B). Both species can be highly variable in size which depends on sex, parasitism and larval developmental conditions (Ryan and Hurley 2012; Kroll et al. 2013; Haavik et al. 2016a), but in North American areas of sympatry, *S. noctilio* adults are usually slightly larger and carry more eggs than *S. nigricornis* (Haavik et al. 2016a; AEH and JCH unpublished data). While *S. noctilio* is more aggressive and can attack healthier trees, both species will oviposit in pines of poor vigor or that are recently dead (see Suppl. material 1: A). The resources needed by these species are ephemeral and often patchily distributed; in agreement, studies have shown that populations of *S. noctilio* are limited by the availability of acceptable pines (Haavik et al. 2016b). To investigate these two *Sirex* species in pines after establishment of *S. noctilio*, we compared the functional traits of *S. noctilio* and *S. nigricornis*. Here, we compare the sizes of venom glands of these two species in relation to female sizes, and their pine species use and voltinism. Using trees with evidence of *S. noctilio* infestation, we present the relative densities of the two *Sirex* species across time, beginning three years after the first detection of *S. noctilio* in the northeastern US. Our goal is to compare functional traits between the native and invasive to begin to understand the effects of the *S. noctilio* invasion on native siricid communities.

Materials and methods

Rearing procedures

Red pines (*Pinus resinosa*) and scots pines (*Pinus sylvestris*) with resin beads characteristic of *S. noctilio* attack (Dodds et al. 2010) were located from October to December in New York and Pennsylvania. These trees were often suppressed and patchily distributed. In spring, infested trees were felled, areas of trunks with resin beads were cut into bolts, and ends of bolts were coated in sealant (Waxlor, Willamette Valley Company, Eugene, Oregon, USA). For the majority of studies, 70 cm long bolts were placed in fiber barrels (91 cm high × 61 cm diam) covered securely with window screening, in an unheated barn. Once adult wasp emergence began (in early to mid-July), barrels were checked daily for two months and then subsequently 3–4 times per week. *Sirex* that emerged were placed in 29 ml clear plastic cups at 4°C. All *Sirex* emerging were identified using characters described in Schiff et al. (2012).

To cover the emergence periods for both *Sirex* species, checking for emergence finished in early November, and, at that time, barrels were completely checked for any additional specimens.

For studies comparing the abundance of *Sirex* species by tree species, *Sirex* were reared from 50 cm long bolts placed in horizontal cardboard rearing tubes. Bolts were spaced from tube sides using nails and were housed at ambient environmental conditions in a screened outdoor insectary. Glass emergence jars were fitted to the tube ends, oriented facing screened windows for a natural photoperiod, and emerging *Sirex* were collected daily.

Adult size and venom gland measurement

To quantify the sizes of emerging adults, we followed Madden (1974) and Nahrung (2016) in using the apical width of the prothorax. Measurements were made using digital calipers (Traceable Products, Webster, Texas, USA). Infection with the parasitic nematode *Deladenus siricidicola* negatively impacts adult size (Kroll et al. 2011; Haavik et al. 2016a), so we diagnosed whether each of the adults being measured was parasitized by these nematodes. Males and females were dissected alive under a dissecting microscope at 10× magnification. The abdomen was removed and cut lengthwise to open it, without damaging the venom glands in females, and presence of nematodes within the abdominal cavity and reproductive tissues was recorded. Eggs from females were counted at 63× magnification and venom glands were removed and immediately weighed on a microscope cover slip.

To compare sizes of *S. noctilio* adults with (n = 92) and without (n = 412) nematodes, we used randomly selected individuals emerging from barrels in 2012–2014. There were far fewer *S. nigricornis* emerging during this period and nematode infections were uncommon in *S. nigricornis*, so analyses included only *S. nigricornis* of both sexes without nematodes (n = 36).

To assess weights of venom glands, a total of 51 *S. noctilio* were randomly selected in 2014–2016 for dissection and 21 of these contained nematodes. Since few female *S. nigricornis* emerged from rearings from the northeast during 2014–2016, 30 *S. nigricornis* females from Arkansas and Louisiana that had been caught in panel traps were used for venom gland weights. We were concerned that these *S. nigricornis* from the southeast both had been flying before being trapped and were from a different geographic region. To test the accuracy of using southeastern *S. nigricornis* as replacements for northeastern *S. nigricornis*, we compared the relationship between numbers of eggs and body size for *S. nigricornis* females collected from traps in the southeastern vs. emerging from wood from the northeastern USA. Southeastern *S. nigricornis* carried the same number of eggs in relation to prothorax width as *S. nigricornis* emerging from wood in the northeastern US ($t = -1.10$; $P = 0.2713$), so we used venom gland weights from southeastern *S. nigricornis* for comparisons.

Table 1. First and second year emergence by *Sirex noctilio* and *Sirex nigricornis*.

	Location	2 years of emergence	Total Sirex emerging	Emergence year 1 (%)	Emergence year 2 (%)	% trees with 2nd year emergence
Sirex nigricornis	Warren County, NY	2013–2014	38	44.7%	55.3%	50.0%
Sirex noctilio	Warren County, NY	2013–2014	15	73.3%	26.7%	25.0%
	Tioga County, PA	2014–2015	1056	98.5%	1.5%	39.1%
	Tioga County, PA	2015–2016	709	89.1%	10.9%	42.9%

Tree species use

Use of *P. resinosa* versus *P. sylvestris* by *S. nigricornis* and *S. noctilio* was quantified using infested trees in northern New York State, with site information in Foelker et al. (2016; Table 1) (2010: 10 *P. resinosa*, 12 *P. sylvestris*; 2011: 22 *P. resinosa*, 10 *P. sylvestris*). Trees were harvested from 21 April – 24 May in 2010 and 31 March – 7 May in 2011 and *Sirex* were reared from trees as described above.

Voltinism

On 4 June 2013, 12 *Sirex*-infested *P. resinosa* were collected from a plantation on River Road, Warren Co., New York (43°31'59.7"N 73°49'30.8"W). Trees were cut into 219 70 cm long bolts and woodwasps were reared as described above, with barrels checked every 1–2 days to collect individuals very soon after emergence; females were never found to be ovipositing when collected this soon after emergence. In November 2013, barrels were thoroughly checked for dead *Sirex* so that any first year emergers were not mistaken for second-year emergers. Barrels were stored in an unheated barn over the winter and were checked for emergence throughout the 2014 flight season. This procedure was repeated for a third year, through the 2014–2015 winter and 2015 flight season. As a continuation to this study, in Tioga Co., Pennsylvania, in spring 2014 we harvested 23 infested *P. resinosa* and, in spring 2015, 29 *P. resinosa*. Wood from trees cut in 2014 and 2015 was maintained and emergence was checked for two years.

Densities and co-occurrence of *S. noctilio* and *S. nigricornis*

Pines with resin beads indicative of *S. noctilio* attack were harvested in central and northern New York State and north-central Pennsylvania and *Sirex* were reared from them. Even within the same region, it was rare that the exact same site was sampled more than one year. *Pinus resinosa* were harvested from plantations in Tioga Co., Pennsylvania yearly, from 2011 and 2013–2015, with 20–30 trees harvested each year. *Sirex* were also reared from mixtures of *P. resinosa* and *P. sylvestris* from natural

forests in northern New York State and from mature plantations in central New York State. In 2007 only *P. sylvestris* was sampled as described in Long et al. (2009). Trees included in analyses were those from which either one or the other or both *Sirex* species emerged.

Data analysis

A general linear mixed model with year as a random effect was used to compare sizes of *Sirex*. To compare body size versus venom gland mass, the significance of difference between slopes was calculated (Cohen et al. 2003). Comparisons of body size across species, sex and nematode parasitism were conducted using mixed models with year as a random effect and least squares means were used for post hoc comparisons (SAS 2014). Because very few *S. nigricornis* were reared that were parasitized by nematodes, comparing body sizes for individuals that were parasitized versus not parasitized was only possible for *S. noctilio*. Tree species use analysis was conducted using a mixed model with (ln +1)-transformed densities by volume of wood for *S. nigricornis* versus *S. noctilio* (SAS 2014). *Sirex* species, tree height, tree diameter and tree species were explanatory variables, with tree nested within site and site as random effects. The interaction of *Sirex* species with tree species was initially included but was removed as it was not significant. Wilcoxon signed ranks tests were used to compare numbers of *S. noctilio* versus *S. nigricornis* adults emerging from trees in 2007–2014.

Results

Trait-based studies: Venom glands and *Sirex* size

Weights of venom glands increased with increasing body size (measured as prothorax width) (Fig. 1) but this relationship differed by species. The slope of the regressions of body size against venom gland weight for *S. nigricornis* without nematodes was less steep compared with *S. noctilio* without nematodes ($t = 4.527$; $df = 56$; $P < 0.0001$); this slope was close to twice as steep for *S. noctilio* compared with *S. nigricornis*. The weight of the venom glands for *S. nigricornis* females without nematodes also was significantly less than for *S. noctilio* with nematodes ($t = 3.3824$; $df = 47$; $P = 0.0015$). *Sirex noctilio* parasitism by nematodes did not significantly affect the relationship between the weight of the venom gland and body size, when compared with non-parasitized *S. noctilio* individuals ($t = 1.1141$; $df = 47$; $P = 0.2709$).

For collections across 2012–2014, on average non-parasitized *S. noctilio* females (prothorax width: 3.90 + 0.83 mm) were larger than *S. nigricornis* females (2.46 + 0.35 mm) ($t = 6.27$; $P < 0.0001$) and non-parasitized *S. noctilio* males (2.92 + 0.83 mm) were larger than *S. nigricornis* males (2.38 + 0.56 mm) ($t = 3.00$; $P = 0.0028$).

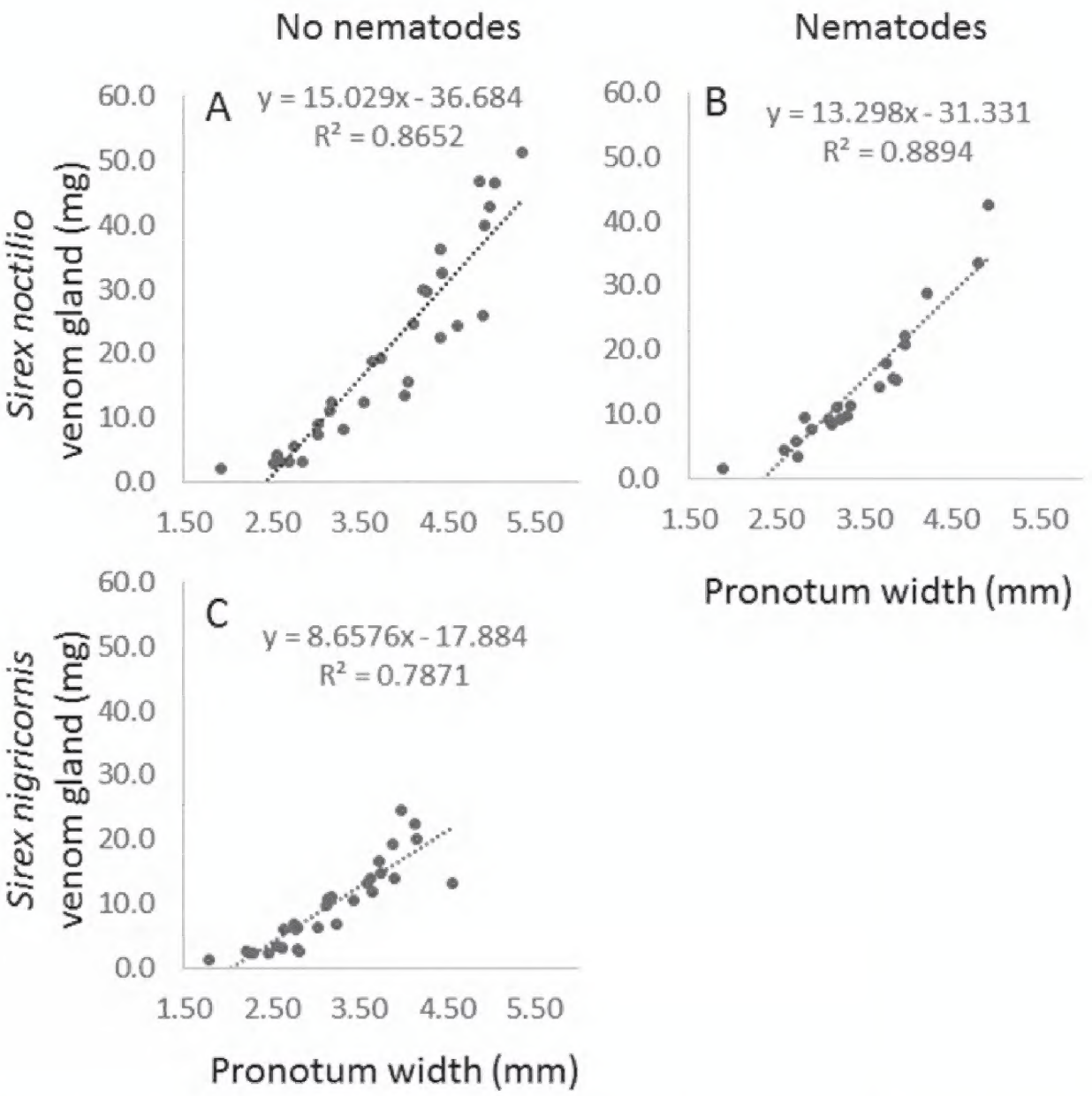

Figure 1. Relationships between venom gland mass and body size, measured as pronotum width, for *S. noctilio* and *S. nigricornis*. *Sirex noctilio* data were analyzed by presence or absence of parasitism by nematodes (*Deladenus siricidicola*) while numbers of *S. nigricornis* parasitized by nematodes were too low for analysis. **A** *Sirex noctilio* females without parasitism by nematodes **B** *S. noctilio* females parasitized by nematodes, and **C** *S. nigricornis* without nematode parasitism.

For male *S. noctilio*, nematode parasitism unexpectedly resulted in larger body sizes ($t = -2.62$; $P = 0.0091$) while this relationship was reversed for females ($t = 2.34$; $P = 0.0195$) (Fig. 2).

Trait-based studies: Tree species preference

Sirex densities by tree species did not differ between the two *Sirex* species ($F_{1,52.6} = 0.01$; $P = 0.9395$). The only main effect that was significant in the model was the comparison of densities of the two *Sirex* species ($F_{1, 56} = 32.11$; $P < 0.0001$; *S. nigricornis* density = $8.9 \pm 2.6/m^3$, *S. noctilio* density = $44.3 \pm 11.5/m^3$).

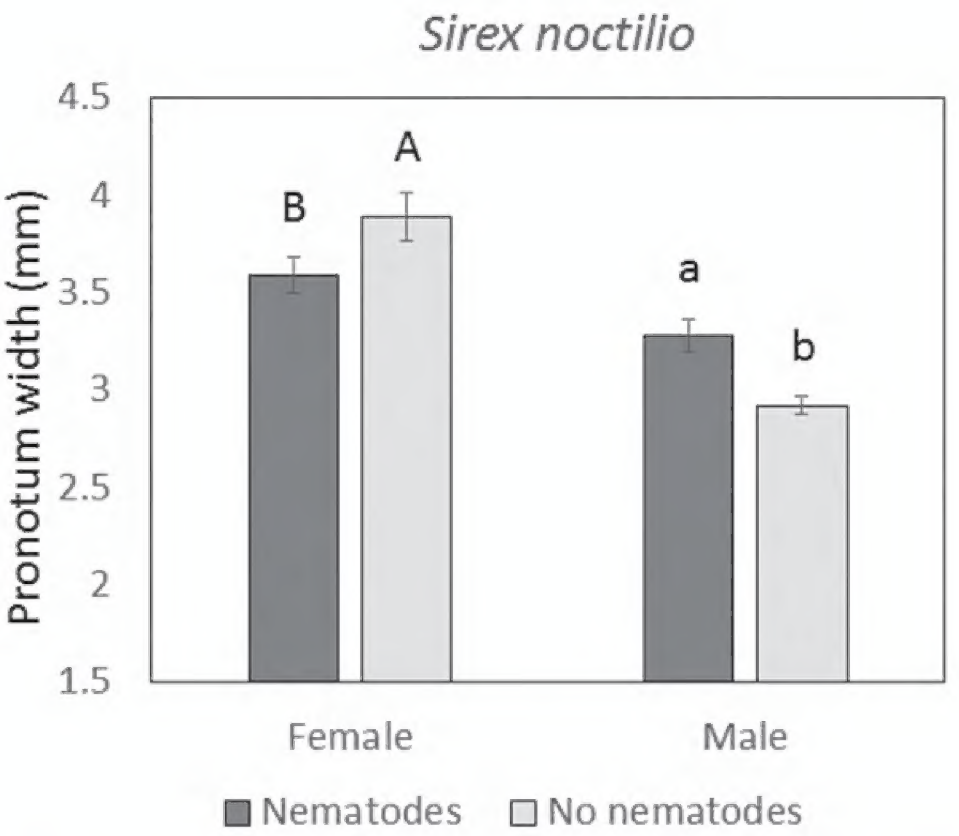

Figure 2. Mean body size (+ SE), measured as pronotum width, for *S. noctilio* males or females parasitized by the nematode *D. siricidicola* or not. Different letters (comparing either capital letters or comparing lower case letters) demonstrate significant differences within sexes.

Trait-based studies: Comparing voltinism

Nearly half of adult *S. nigricornis* emerged from wood during the first season in our rearings, over half emerged during year 2 (Table 1), and no *S. nigricornis* emerged during year 3. In contrast, emergence of *S. noctilio* adults primarily occurred in year 1 (Table 1). Numbers of *S. noctilio* emerging from wood in 2013–2014 were low but among these, 26.7% emerged during the second year. For wood harvested in 2014 or 2015 and reared for two years, from 1.5% to 10.9% of the *S. noctilio* emerged during year 2.

Densities and co-occurrence of *S. noctilio* and *S. nigricornis*

Between 2010 and 2015, *S. nigricornis* densities were lower than densities of *S. noctilio* in central New York State and north central Pennsylvania, where most pines that were sampled had been purposefully planted (Table 2). However, when sites in central and northern New York State were sampled within 2–3 years of the first reports of *S. noctilio* in those areas (see Table 2 footnotes), numbers of *S. nigricornis* emerging did not differ significantly from *S. noctilio*, although they were usually numerically lower. When *S. nigricornis* emerged, they more commonly co-occurred in the same trees as *S. noctilio* and rarely were the only *Sirex* species emerging from a tree. In 2015, no *S. nigricornis* emerged from infested material from north central Pennsylvania and during this study, densities of *S. nigricornis* from this same area were always low.

Table 2. Co-occurrence and densities of *S. noctilio* and *S. nigricornis* emerging from *P. sylvestris* and *P. resinosa* from New York and Pennsylvania, 2007-2015 (only including trees from which *Sirex* emerged).

	Total infested trees sampled	Tree species[a]	Total trees with only *S. noctilio*	Total trees with only *S. nigricornis*	Total trees with both *Sirex* species	Mean *S. noctilio*/tree ± SE	Mean *S. nigricornis*/tree ± SE	P values[b]
Central New York State[c]								
2007	6	S	3 (50%)	0 (0%)	3 (50%)	218.8 ± 64.9	13.2 ± 10.4	0.0625
2010	9	SR	6 (67%)	1 (11%)	2 (22%)	41.8 ± 9.8	1.6 ± 0.9	0.0117 *
2011	19	SR	12 (63%)	0 (0%)	7 (37%)	48.2 ± 14.9	5.5 ± 3.0	<0.0001 *
Northern New York State[d]								
2010	13	SR	3 (23%)	3 (23%)	7 (54%)	13.4 ± 4.8	20.2 ± 6.5	0.5532
2011	8	SR	4 (50%)	2 (25%)	2 (25%)	17.7 ± 5.7	3.7 ± 1.8	0.1641
North Central Pennsylvania[e]								
2011	19	R	15 (79%)	0 (0%)	4 (21%)	38.4 ± 10.3	0.7 ± 0.4	<0.0001 *
2013	17	R	12 (71%)	1 (6%)	4 (24%)	22.8 ± 6.0	1.6 ± 1.2	0.0001 *
2014	26	R	22 (85%)	0 (0%)	4 (15%)	52.5 ± 10.7	0.7 ± 0.5	<0.0001 *
2015	15	R	15 (100%)	0 (0%)	0 (0%)	22.8 ± 7.4	0.0 ± 0.0	<0.0001 *

[a]S = scots pine (*P. sylvestris*), R = red pine (*P. resinosa*), SR = mixture of scots and red pines.

[b]Wilcoxon ranked sign tests comparing numbers of *S. noctilio* versus *S. nigricornis* emerging from trees. Asterisks indicate significantly different results, with more *S. noctilio* than *S. nigricornis*.

[c]*S. noctilio* first collected in this area in 2004 and 2005 (Dodds and de Groot 2012).

[d]*S. noctilio* first collected in this area in 2008 (AEH unpubl. data).

[e]*S. noctilio* first collected in this area in 2008 (B. Regester, pers. comm).

Discussion

Comparing functional traits

The overall body sizes of *S. noctilio* as well as the sizes of their venom glands were significantly larger than the bodies and venom glands of the native *S. nigricornis*. The venom glands of *S. noctilio* are also larger than those of seven other European siricids (Spradbery 1977) and experimentation has shown that venom from *S. noctilio* had greater phytotoxic activity than venom of these European siricids (Spradbery 1973). While a key component of the venom in the *S. noctilio* gland has been characterized as noctilisin (Bordeaux et al. 2014), the identities of compounds in the venom glands of *S. nigricornis*, or glands of any other siricids, are not known (Wang et al. 2016). Regardless, the fact that the *S. noctilio* venom glands are larger (relative to adult body size) than venom glands known from other siricids is consistent with the fact that this is the most aggressive siricid, reported as able to kill relatively healthy pines where it is adventive (see Suppl. material 1: A), while other woodwasps are considered relatively benign secondary pests in forests (Schiff et al. 2012).

Haavik et al. (2016a) found that *S. nigricornis* carries more eggs per body size than *S. noctilio* and our studies have documented the same trend (AEH and JCH, unpublished data). However, the present study demonstrated that on average *S. noctilio* females with or without nematode infections were larger than *S. nigricornis* females and the same relationship holds for males. So, although *S. nigricornis* has the potential to carry more eggs than *S. noctilio*, when we calculated the numbers of eggs per female based on sizes of females that emerged from wood in our studies, using the regression equations in Haavik et al. (2016a), the number of eggs for average-sized *S. noctilio* female was 166 but 138 eggs would be produced by *S. nigricornis*. Thus, the larger body size of *S. noctilio* emerging from trees compensated so that on average females of the invasive carried more eggs than *S. nigricornis*. It was unexpected that while nematode-infected *S. noctilio* females were smaller than healthy females, nematode-infected males were larger than healthy males, an association also found by Haavik et al. (2016a).

The densities of the two *Sirex* species emerging from *P. resinosa* and *P. sylvestris* did not differ by tree species. Studies have found a trend of *P. sylvestris* being colonized more frequently by *S. noctilio* compared with *P. resinosa* (Dodds et al. 2010; Foelker 2016) and *S. nigricornis* was not included in those studies. Largely based on the southern hemisphere where many North American pines have been introduced, susceptibility of pine species to *S. noctilio* varies by tree species (Ryan and Hurley 2012; Nahrung et al. 2015). Our result was somewhat unexpected because *P. sylvestris* is native to Europe, where it is assumed to have coevolved with *S. noctilio* (Ayres et al. 2014). However, we do not know exactly where the genotypes of *S. noctilio* introduced to New York and Pennsylvania originated and, given the broad native geographic range of *S. noctilio*, it is possible that these genotypes of this woodwasp did not co-evolve with *P. sylvestris* (Boissin et al. 2012; Bittner et al. 2017). On the other hand, *P. resinosa* and *S. nigricornis* co-evolved in North America and in this case there was no preference for the native pine over the introduced pine.

Sirex noctilio and *S. nigricornis* also differed significantly based on the percentages of the populations emerging from wood after 1 vs 2 years. In our studies, *S. noctilio* mainly emerged in year 1; from 1.5–27.7% of *S. noctilio* emerged the second year (Table 2) while in Ontario, Ryan et al. (2012b) found 2.2% emergence during year 2. Second-year emergence of *S. noctilio* was 15–25% in New Zealand and Australia, including Tasmania (Morgan 1968; Taylor, 1978), 1.6% in Eurasia (Spradbery and Kirk 1978), and 24% in Galicia, Spain (Lombardero et al. 2016). In all cases, percent emergence for *S. noctilio* in the second year of rearing was less than that recorded for *S. nigricornis* in our study, for which close to 50% emergence occurred in both years 1 and 2. Differences in voltinism between *S. noctilio* and *S. nigricornis* could have large impacts on their population dynamics. Based on our results, future studies of *S. nigricornis*, at least in northeastern North America, should allow two years for emergence from infested wood.

Comparing abundance of *Sirex* species

In northeastern North America *S. noctilio* is now the most abundant woodwasp attacking pines (Long et al. 2009; Ryan et al. 2012a; Foelker et al. 2016). Unfortunately, there are no records of the population densities or tree use by *S. nigricornis* before *S. noctilio* arrived but now, use of suppressed pines by *S. nigricornis* is much less than use of this resource by *S. noctilio* (e.g., Table 2).

Sirex noctilio has a temporal advantage over *S. nigricornis* as many emerge 1–2 months before *S. nigricornis*, although there is overlap in emergence between these species in northeastern North America (Ryan et al. 2012a; Haavik et al. 2013; Hartshorn et al. 2016; Suppl. material 1: B). *Sirex noctilio* is found colonizing trees at higher densities than *S. nigricornis*. Therefore, each year *S. noctilio* will occupy what is considered as being their preferred resources (i.e., suppressed trees that are not yet dead; see Suppl. material 1: A) before *S. nigricornis* adults have emerged. Among all pines from which *Sirex* were reared, only *S. noctilio* emerged from 56% (across the 9 years of this study). However, after the invasive had been present for a few years in an area, when the two species both emerged from trees, numbers of *S. nigricornis* were lower than *S. noctilio* and we very rarely found only *S. nigricornis* emerging from a tree. Based on the low numbers of *S. nigricornis* emerging from infested trees, we hypothesize that population densities of *S. nigricornis* emerging could be low because when adults of the native species emerge, the transient resource of suppressed trees had already mostly been exploited. However, *S. nigricornis* could have an advantage in situations where pines unacceptable to *S. noctilio* for some reason could be available for use by *S. nigricornis* or when pines could become weakened (e.g., by lightning strikes) after the main flight of *S. noctilio* adults and before or during the *S. nigricornis* flight time. In addition, the fact that the transient resource of suppressed trees are often patchily distributed (e.g., Ayres et al. 2014) could lead to coexistence of these species via differential spatial distribution of use of suppressed pines.

Monceau et al. (2015) have shown that some degree of niche differentiation between native and invasive hornets can minimize competition. We did not sample recently dead trees in this study but experiments have shown that *S. nigricornis* will oviposit into wood from trees that have recently been cut, although oviposition was minimal as soon as 30 days after cutting the wood (Hartshorn 2012). We do not know to what extent *S. noctilio* will choose to oviposit in wood from recently cut trees but when siricids were reared from diverse types of wood sampled over eight years from Europe, Turkey and North Africa, *S. noctilio* only emerged from samples from standing trees and timber and never from fallen trees or wood on the ground (Spradbery and Kirk 1978). While niches of these two *Sirex* species probably differ to some extent relative to the health or condition of pines that are preferred or acceptable for oviposition and development, there is also niche overlap (see Suppl. material 1: A). Based on relative densities and traits, we hypothesize that after the invasion of *S. noctilio*, *S. nigricornis* could develop in suppressed trees less often than prior to the invasion and the native might now more frequently use recently fallen, dead trees, as *S. noctilio* would have already exploited the majority of standing suppressed pines. Alternatively, suppressed pines further weakened by *S. noctilio* attack could at times provide an increased resource for *S. nigricornis* populations. Knowledge about normal densities of *S. nigricornis* before invasion by *S. noctilio* is necessary to further understand the impact of the native on the invasive woodwasp. In addition, further studies investigating the health of pines associated with oviposition and development of these two *Sirex* species are needed to clarify the overlap in niches of these two species with regard to tree health.

Conclusions

In this study, we investigated aspects of the biology and ecology of these now-sympatric native and invasive siricids toward predicting the impact *S. noctilio* might be having on this congeneric native species also utilizing suppressed pines (Suppl. material 1: A). The invasive *S. noctilio* uses the same tree species as the native *S. nigricornis* but venom glands of *S. noctilio* are larger. Although *S. nigricornis* carries more eggs than *S. noctilio* per body size, *S. nigricornis* adults are significantly smaller than *S. noctilio*, resulting in greater fitness for *S. noctilio*. In other systems, fecundity has been shown to be an important functional trait for predicting success of invasives (e.g., Boivin et al. 2008; Capellini et al. 2015). In addition, the phenology of the invasive and its faster speed of development also allow *S. noctilio* to exploit common resources before *S. nigricornis.*

We cannot definitively answer to what extent the presence of *S. noctilio* results in more or less habitat in which *S. nigricornis* can develop. Little is known of the biology and ecology of *S. nigricornis* but we know that it will oviposit and develop in pines already attacked by *S. noctilio*. Attacks by *S. noctilio* could create more suppressed trees acceptable to *S. nigricornis* by pre-injecting the symbiont plus venom and thereby disabling tree defenses and thus creating more habitat for *S. nigricornis*. However, abundance data suggest that few *S. nigricornis* emerge from trees that they co-inhabit

with *S. noctilio*. As an alternative, since *S. noctilio* mostly flies and oviposits before *S. nigricornis*, perhaps this invasive attacks the best of the transient resource of weakened trees that could potentially be used by either species and *S. noctilio* thus uses most of this resource before *S. nigricornis* adult females would have emerged to oviposit. The extent that co-occurring *S. nigricornis* and *S. noctilio* will compete for recently dead trees remains to be determined. Further data documenting the ecology and naturally occurring densities of *S. nigricornis* in the southeastern US, where pine forests are extensive, will assist with predicting to what extent *S. nigricornis* niches and abundance will be altered when *S. noctilio* spreads into this region.

Acknowledgments

We thank Brad Regester, Bill Laubscher and Tim Marasco, Pennsylvania DCNR Bureau of Forestry for assistance with infested wood from north central Pennsylvania, Jim Meeker, Wood Johnson, Jessica Hartshorn and Fred Stephen for providing *S. nigricornis* from Louisiana and Arkansas, and USDA APHIS for assistance with obtaining *S. noctilio*-infested wood in 2007. Francoise Vermeylen assisted with statistical analyses and we thank Flora Krivak-Tetley, David Harris, Stefanie Kroll, and Sandy Liebhold for assistance with this manuscript. This work was supported by USDA Forest Service Cooperative Agreements granted to AEH.

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Supplementary material 1

A. Association between health of pines and response by *S. noctilio* and *S. nigricornis*; B. Emergence of *S. noctilio* and *S. nigricornis* from pines collected from New York and Pennsylvania in spring 2012

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Data type: Microsoft Word Document (.docx)

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Link: https://doi.org/10.3897/neobiota.36.14953.suppl1